Evidence of Gregarious Settlement in the Larvae of the Marine Snail *Collisella strigatella* (Carpenter)

BY

JOHN DIXON

Department of Biological Sciences, University of Southern California
Los Angeles, California 90007

INTRODUCTION

THE LARVAE OF MANY INVERTEBRATES settle selectively on substrates with particular physical or biological characteristics (THORSON, 1964; MEADOWS & CAMPBELL, 1972; CRISP, 1974, 1976, 1979; SCHELTEMA, 1974). The tendency of some larvae to settle in response to the presence of individuals of their own species is called "gregarious settlement" (CRISP, 1974). Gregarious settlement has been documented by means of field or laboratory experiments for several species of sessile marine invertebrates: a bivalve mollusc (COLE & KNIGHT-JONES, 1949), barnacles (KNIGHT-JONES & STEVENSON, 1950; KNIGHT-JONES, 1953a), polychaetes (KNIGHT-JONES, 1951, 1953b; WILSON, 1968; STRAUGHAN, 1972), a bryozoan (WISELY, 1958), a hermatypic coral (LEWIS, 1974), and a tunicate (YOUNG & BRAITHWAITE, 1980).

There apparently have been few studies of this phenomenon in mobile species. I know of only one case in which gregarious settlement in a mobile species was experimentally demonstrated. KISELEVA (1967) studied two species of gastropods, *Rissoa splendida* Eichwald and *Bittium reticulatum* (da Costa), which live on algae, particularly of the genus *Cystoseira* C. Agardh. In her laboratory experiments both snails settled preferentially on algae (mostly *Cystoseira)* and near young of their own species. In other experiments she showed that the larvae recognized both the algal substrate and other individuals of their own species by means of a chemotactile sense.

Here I present evidence which suggests that larvae of the intertidal limpet, *Collisella strigatella* (Carpenter, 1864), also recognize and selectively settle near adults of their own species.

METHODS

Collisella strigatella is one of several species of acmaeid limpets which live on hard substrates in the intertidal zone along the California coast. In the vicinity of Santa Barbara its local distribution overlaps those of three other abundant species: *Collisella digitalis* (Rathke, 1833), *Collisella scabra* (Gould, 1846), and *Notoacmea fenestrata* (Reeve, 1855). All these species graze the thin film of diatoms and juvenile stages of macroalgae which cover intertidal rocks. In the lower and middle intertidal zones, *C. strigatella* and *N. fenestrata* are the most abundant limpets on boulders less than about 50 cm high which have much open space (DIXON, 1978).

I censused limpets in boulder fields at Arroyo Hondo about 50 km west of Santa Barbara, and at Toro Canyon, about 8 km east of Santa Barbara. At these locations the boulders are set in sand and migration is generally not possible. I estimated the areas of boulders by dividing them into regular plane figures with chalk, measuring the appropriate dimensions, calculating the areas, and summing them. Based on observed changes in size frequency distributions with time, *Collisella strigatella* less than 6 mm in shell length probably settled within about 4 months of the census. I treated these as recently settled young and larger animals as representing cohorts from previous settlement seasons and did a correlation analysis of the densities of the two size classes. For this analysis I used data from those sampling periods when recently settled young were most numerous.

At Arroyo Hondo I fenced square areas, 15 cm on a side, with plastic mesh (VEXAR, Dupont Corp.) on a large, flat rock located about +0.15 m (+0.5 ft) in the

intertidal zone. The fenced area was covered with the typical film of diatoms and patches of crustose corallines. There was no apparent difference among fenced plots and treatments were completely randomized among plots. Within each fenced plot, I confined 10 limpets in the following species combinations: 10 *Collisella strigatella* alone; 5 *C. strigatella* with 5 *Notoacmea fenestrata;* or, 10 *N. fenestrata* alone. There were 4 replicates of each treatment. All the adults were about the same shell length (*C. strigatella*: $\overline{X} = 10.1$ mm; *N. fenestrata*: $\overline{X} = 10.8$ mm). In October 1976 there were many newly settled limpets within the fenced plots. All were less than 4 mm in shell length and many were around 2 mm long. All the animals which were large enough to identify to species were *C. strigatella.* The smallest individuals were either *C. strigatella* or *N. fenestrata,* but were not distinguishable in the field even with the use of a hand lens. However, they were distributed among treatments in the same proportions as the identifiable recruits and the following observations indicate that they were also *C. strigatella*: 1) *N. fenestrata* generally settle earlier in the year (Fritchman, 1961; Dixon, 1978); 2) On 34 boulders in the same area as the experimental boulder there were 45 *C. strigatella* less than 4 mm long but only 3 *N. fenestrata,* and; 3) Based on growth rate data (Dixon, unpublished), *N. fenestrata* that were about 2 mm long in October would have been large enough to identify in November but still in the 0-4 mm size class, or perhaps the 4-8 mm class. However, on 29 boulders censused in November there were no *N. fenestrata* less than 4 mm long and only 5 between 4 and 8 mm. Therefore, I included all the new recruits in the experimental plots in the analysis and compared the three treatment means using a one-way analysis of variance and a least significant difference test for *a posteriori,* pair-wise comparisons.

RESULTS AND DISCUSSION

Within boulder fields the density of small, recently settled *Collisella strigatella* on boulders isolated in sand is positively correlated with that of older individuals (Table 1). Since the sand prevents migration, this pattern must result from events taking place at the time of settlement or shortly thereafter. In the absence of migration, and given constancy in the suitability of habitat, a correlation between the density of adults and young is necessary, though not sufficient, evidence of gregarious settlement. The pattern could also be caused by mortality of recently settled larvae in unsuitable habitats, or by selective settlement in response to other biological or physical characteristics of boulders to which the adults had also responded.

The results of the experiment involving fenced adults suggests that the larvae respond to conspecific adults. The analysis indicates that newly settled *Collisella strigatella* occurred in greater numbers in those fenced plots that contained adults of the same species than in plots which contained only adults of the related species, *Notoacmea fenestrata* (Table 2). The only difference between these plots was the species composition of the adults. Nevertheless, since the larvae were not observed at the time of settlement, the results can be interpreted in several ways: 1) the larvae settled randomly with respect to the adults of the two species but suffered greater mortality in plots containing only *N. fenestrata*; 2) the larvae settled randomly with respect to the adults of the two species but dispersed out of the plots containing only *N. fenestrata,* or; 3) the larvae recognized and selectively settled near adults of their own species. The first hypothesis can be rejected on the basis of the experimental results—recruits were as numerous in plots in which half the adults were

Table 1

Correlation between the density of small and large limpets, *Collisella strigatella,* in two southern California boulder fields. The small limpets were all less than 6 mm in shell length and probably had settled within about four months of the census.

Location	Date of census	Number of boulders censused	r	P
Arroyo Hondo	07/10/76	30	+ 0.37	< 0.05
Arroyo Hondo	07/03/77	57	+ 0.48	< 0.01
Arroyo Hondo	11/14/77	48	+ 0.45	< 0.01
Toro Canyon	12/12/77	42	+ 0.34	< 0.05

Table 2

Effect of the presence of previously settled individuals of the same and of a related species on the recruitment of *Collisella strigatella.* Limpets (ca. 10 mm shell length) were confined in fenced plots in three species combinations: 10 *C. strigatella* alone; 5 *C. strigatella* with 5 *Notoacmea fenestrata,* and; 10 *N. fenestrata* alone. After a settlement episode the number of recently settled *C. strigatella* in each plot was counted. The lines connect means which are not significantly different by a Least Significant Difference test ($\alpha = 0.05$).

Treatment	Mean number of recruits
5 *C. strigatella* and 5 *N. fenestrata*	12
10 *C. strigatella*	10
10 *N. fenestrata*	4

Analysis of variance

Source of variation	DF	SS	MS	F	P
Treatment	2	158	79.0	37.6	< 0.001
Error	9	19	2.1		
Total	11	177			

N. fenestrata as in plots in which the latter were absent. That the results could be due to selective migration soon after settlement cannot be rigorously ruled out since it was probably possible for very small limpets to move through the fences. However, since newly settled individuals were abundant in the mixed species plots, they were apparently not reacting negatively to the presence of *N. fenestrata.* On the other hand, adults of both species were present on the unfenced portions of the rock and the new recruits may have sought out conspecific adults outside the plots. Although this is a possibility, I think the fences would have been a serious barrier to migration. The interpretation of the experimental results that I find most compelling is the third: *Collisella strigatella* recognize and selectively settle near individuals of their own species.

Although the results of both censuses of islands of habitat and the field experiment suggest gregarious settlement, this remains a hypothesis to be tested further. The definitive test must await the successful culturing of these larvae since it requires exposing competent larvae to appropriate substrates in the presence of adults of the same and of different species (cf. Kiseleva, 1967; Cameron & Schroeter, 1980).

If *Collisella strigatella* settle gregariously, one wonders why the correlation between the density of adults and newly settled individuals is not higher. It is probably because the habitat on a given boulder often changes significantly in a relatively short time. For example, barnacles settle and grow on boulders where they were previously absent, or disappear from rocks on which they were once abundant. As a result, a boulder may be a more or a less suitable habitat during a given settlement episode than when the adults settled (Choat, 1977; Dixon, 1978). Despite this phenomenon, gregarious settlement could aid species like *C. strigatella* in the selection of a suitable habitat because of the tremendous variability in environmental conditions within the intertidal zone. Even physically identical boulders are very different habitats when located at different tidal heights. Limpets which settle on boulders high on the shore are subject to severe physiological stress from drying conditions. Those which settle on boulders in the low intertidal are at a greater risk of being eaten by sea stars or having space preempted by sessile species (Dixon, 1978). Within a given tidal zone there are also significant, and less predictable, variations in environmental conditions. For example, some areas are much more subject to seasonal influxes of sand. In those areas boulders may periodically be completely buried whereas similar boulders 30 m away will remain uncovered. For animals like limpets which live on islands of substrate that occur over a greater range of environmental conditions than is suitable for the species, the presence of conspecific adults is probably one of the best indications of a congenial habitat.

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